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7.—Natural distribution and speciation of marine animals

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Introduction

Descriptive analyses of the distribution of marine animals have been given by many workers, the broadest approach being that of Ekman (1953). He brought together separate analyses by other workers to produce the first world-wide synthesis of animal distribution in the sea in his book entitled, "Zoogeography of the sea". Since that time his definition and terminology of marine zonation both horizontal and vertical have been virtually unchallenged and the book remains one of today's major references.

But Ekman's book was purely descriptive and gave little indication of the mechanisms which originally produced and then maintained the zones as relatively discrete units. His explanation for the separate tropical shallow water faunas are clear enough where physical land bridges exist, i.e. the Panama and South-West Asian land bridges; but "oceanic barriers", although undisputed for many species, receive a circular explanation. He defines the fauna he is comparing as shallow water, tropical stenothermal species with short-lived larvae and, by definition, it follows that passive or active migration across or around the "East Pacific Barrier" or the "Mid-Atlantic Barrier" are impossible for the animals with those attributes.

But what happens if species do have long-lived larvae? One would expect satisfactory occupation in another faunal zone, if the ability to cover large distances were the only necessity to conquer the barrier. The spiny lobster *P. penicillatus,* because of its long pelagic larval life, is able to cross the East Pacific Barrier, but it does not "compete" with the East Pacific mainland species of spiny lobster at all, living only on the offshore islands, e.g. Galapagos, Clipperton, Cocos (Holthuis & Loesch 1967). This species of spiny lobster (and the "Transpacific" fish of Briggs 1961) are "barrier breakers" but do not form part of the fauna on the other side of the barrier. I submit that each species of the fauna on the "other side" is living in environmental conditions to which each has evolved by natural selection and which are incompatible to the "barrier breaking" species. Ekman also mentions the importance of the marine climate to faunas but only in a negative manner of "climatic deterioration". I suggest that climate acts positively in the shaping of faunas by direct and continual selection of each species at all growth stages from egg to adult.

As is already evident, I will draw on spiny lobsters (Palinuridae) for the examples in this address on natural distribution and speciation in the sea. Some of the assumptions I have made are as follows:

1. The principles of speciation (and all biological activity) apply equally as well to marine as to the terrestrial situation.
2. Coexistence of phylogenetically similar species necessitates the existence of separate sets of environmental parameters (habitats). (Scientists must consciously break from their airconditioned houses, laboratories and cars to define those habitats for each species studied).
3. Climatic conditions (of sea and land) determine the spatial distribution of animals; changes in the distribution pattern of these climatic zones in the world result in similar changes in the geographic distribution of animals.
4. All members of each species throughout their lives are continually influenced by the climatic events of nature, and survival or extinction of species result from its ability to find and inhabit suitable environmental situations (natural selection).

The following questions are very important in the study of marine speciation:

What are the earth's basic biological factors?

What is the marine environment?

What are ways in which the marine environment can change with time?

What are the environmental parameters of paramount importance to the species selected for study?

What have been the effects of past environmental changes in the evolution of the species studied?

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The earth's basic biological factors

The basic attributes of this planet are naturally of major significance to every animal (and plant) living on earth: These are:

Solar radiation—this is the energy source.

Water—this acts as a solvent for all biochemical processes.

Dissolved gases—oxygen and carbon dioxide are the gases most important biologically.

Dissolved chemicals—these are the salts and trace elements taken up by animals in solution from the earth.

At any given location on earth the supply of these factors is comparatively constant since direct solar radiation is a function of latitude and the regional distribution of gases and chemicals depends on the distribution of water (rain for terrestrial animals and oceanic circulation for marine animals). The combination of the amounts of all these basic factors in any region of the earth determines the natural environment of that region. In each different environment animals become isolated since each is selected by nature for the particular different combination of environmental factors.

But because of the unequal distribution of heat on the earth's surface, the major earth's media (air and sea) are constantly on the move. Wind belts and ocean currents disturb the animal's environment (described above in static terms). And the animals have evolved particular biological attributes of morphology, behaviour and physiology which are geared to the changes of the environment. Fortunately for the animals, changes in the environment are fairly predictable and it is only when very unusual seasonal events occur that whole communities are wiped out.

This regularity of change of the basic environments is more usually described for terrestrial animals as "the climate" and throughout the world climatic zones and regions are recognised not only by the meteorologists but by the animals too. Scientists who study and recognize these "animal zones" are termed zoogeographers.

In the sea, however, the equivalent of the terrestrial environmental factors of wind, pressure, temperature which make up the climate are not fully reconciled and so no one has been able to forecast the weather under the surface of the sea like they can above it. What is worse is that after an obvious marine meteorological event has occurred, few workers can give reasons for its happening. Bjerknes (1966) has presented a very nice correlation of water circulation abnormalities and abnormalities of the weather patterns *over* land and sea but how these effects were produced is not known.

The marine environment

The total marine environment is as diverse as we find on the land and is certainly not a uniform and unchanging large volume of salty water. The animals living in it have evolved to meet the many different environmental situations of the sea and have become isolated in some cases by the same sort of physical barriers that we observe on land. In Figure 1a, a diagrammatic section of the land and sea illustrates some of these isolated situations. The isolation provided by mountain tops, alpine lakes, mountain slopes, coastal plains and coastal lakes are mirrored, below the sea in the figure, as abyssal trenches, slope basins, continental slopes, continental shelves and continental basins. This analogy is applicable to the bottom living marine animals where physical features provide the isolating mechanisms. But for free swimming or free floating marine animals isolating mechanisms operate through the discreteness of water masses. Brinton's work (1962) serves as an example. He showed not only a correlation of his pelagic euphausids with separate water masses and oceanic circulation patterns but discussed the possible evolutionary significance of changes in those patterns. The pelagic larvae of spiny lobsters are similarly dependent upon oceanic patterns for their survival and eventual return to the region occupied by the parent stock.

The differences between these water masses are quite well recognised by oceanographers and animals alike; in fact oceanographers can identify and even age a particular part of the water column by its physical and chemical characteristics. On this basis, the Indian, Pacific, Atlantic and Antarctic Oceans are very distinct indeed.

Coastal animals, whether free swimming or bottom living, have their basic oceanic environments markedly influenced by the adjacent land. Sediments of particular sorts are carried by wind or river into the coastal waters, salinity will be altered by adjacent rivers (lower salinities) or by adjacent deserts (higher salinities) and the local water circulation pattern is determined by the coastal configuration. One wonders what the biological effects will be when the Central American Seaway is completed. Rubinoff (1968) has proposed the biological problem and has pointed to many of the differences between the Atlantic and Pacific coastal waters of Central America.

Figure 1b shows a section through the coastal shelf indicating the factors influencing the region occupied by the bottom dwelling spiny lobster. All these factors vary in amount with time and the combinations of these factors produce the seasonal marine climate for a particular animal. For coastal animals, there are seasons of rainfall and drought on the adjacent land which vary the run off into the sea and there are similar seasons of oceanic water circulation; changes in the position, direction or intensity of flow of a current will seasonally affect the environment of a fixed or slow moving bottom living animal. Also seasonal solar variations produce regular changes in food resources via plankton activity. Such short term seasonal changes are analogous to the conditions which are found on land and which form the terrestrial climate.

Environmental change

In the past, however, the magnitude of changes has been much greater than those we observe today as seasonal events. All the marine climatic factors illustrated in Figure 1b would have been affected by changes in the position of wind belts, oceanic circulation, upwelling, exchange of

TABLE 1

Distribution of water " types " compiled from the vertical sections of temperature and salinity given in Marshall 1958 *pp.* 53 *and* 55 *for Western Atlantic Ocean*

Approximate depth range (metres) and marine zone	Approximate percentage of total volume	Temperature °C	Range °C	Salinity °/₀₀	Range °/₀₀
Surface—250 Subtropic and Tropic	3	>20	16	30–37	7
Subsurface—1000 Subpolar and Temperate	11	4–20	16	35.0–36.0	1.0
1000–4000 } Polar	75	1–4	3	34.6–35.0	0.4
Antarctic Cell 500–4000 } Polar	11	<1	2	<34.6	very small

oxygen at the surface, evaporation, terrestrial run-off and sedimentation. The importance of solar radiation as the prime controller of the climate in the sea and on the land must be stressed and I submit that through this control, solar radiation is and always has been the key factor in determining the distribution and speciation of animals on the earth.*

When attempting to evaluate what the response of marine species might have been to environmental changes in the past, it is very important to have some concept of the relative stability and geophaphic extent of the water mass inhabited by the species under consideration. In Table 1 the proportions by volume of waters with selected characteristics of salinity and temperature have been assessed. On the percentage by volume, the proportion of the tropical and subtropical waters is very small indeed—only 3%. The combined temperate and subpolar waters are about 11% but the polar waters are 86% of the total, part of which (about 11%) can be clearly recognised as Antarctic water. Any changes that occur to the earth's environment must affect the relatively small volume of surface waters of the tropics and subtropics much more quickly and to a greater degree than the large volume of the subsurface waters.

Climate and spiny lobsters

Figure 2 illustrates the Australian climatic regions, the Australian coastal sedimentation zones and the distribution of the marine spiny

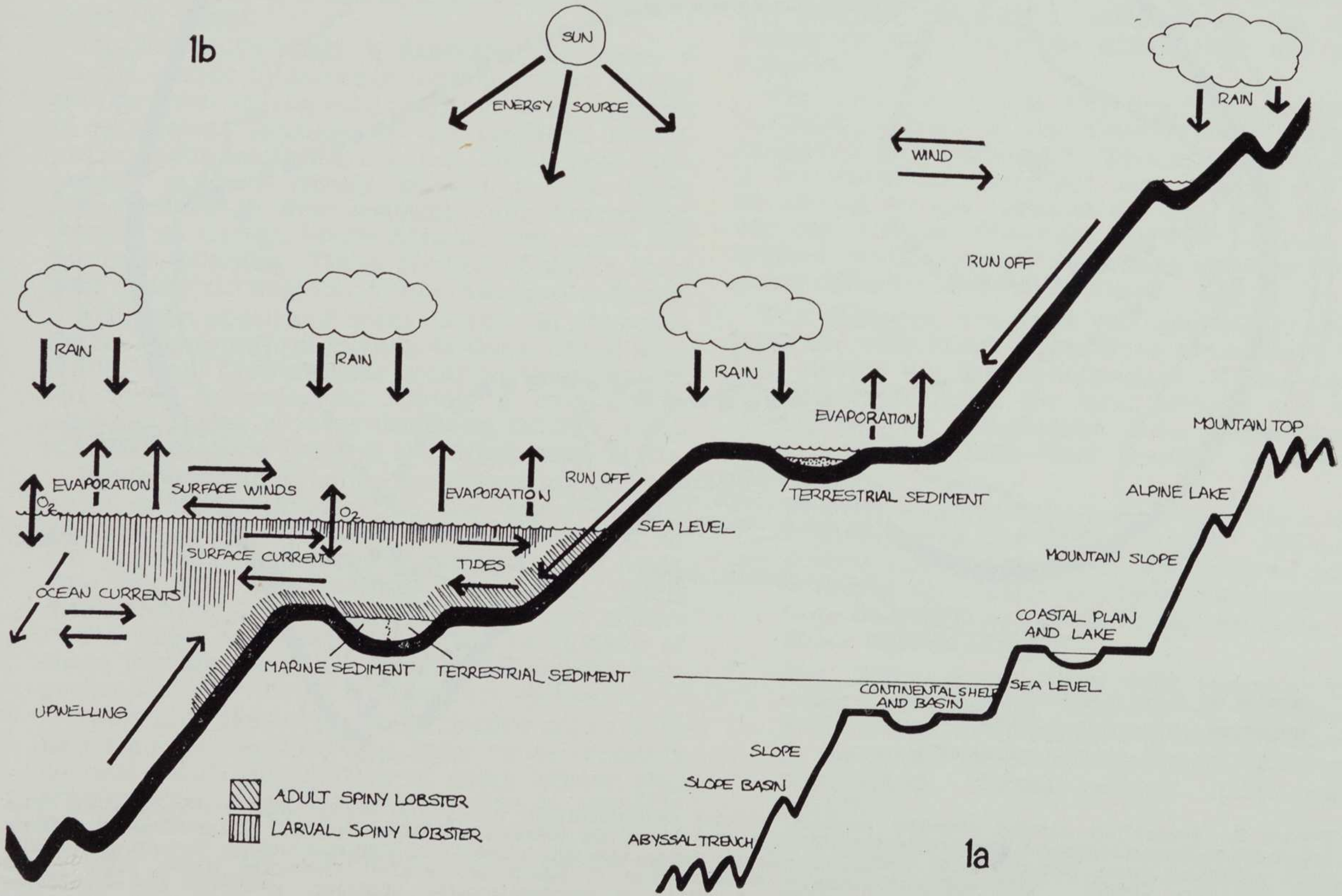

Figure 1.—Comparison of terrestrial and submarine conditions. 1a. Diagramatic section showing some analagous situations above and below sea level. 1b. The influence of climate on marine habitats with particular reference to the coastal and shelf regions inhabited by spiny lobsters.

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*One of the most illuminating studies on long-term variation in solar radiation takes into account past changes in the spatial distribution of earth, sun and moon (Steiner, 1967).

lobsters in the coastal waters; a correlation of major zones is readily observed. Approximate localities where the most rapid change occurs are Frazer Island (Queensland), Bass Strait (Tasmania), and North West Cape (Western Australia). At these places major changes occur in climate, coastal sedimentation and species composition of spiny lobsters.

There are also minor but significant breaks in the patterns at Derby in the north west of Western Australia characterised by climatic change and an apparent "barrier" to the westward movement of a spiny lobster *P. polyphagus*. The break at the south west corner of Australia (about Cape Leeuwin) is signified by the meeting of two spiny lobster species *P. cygnus* and *J. novaehollandiae*. This is probably a reflection of the coastal marine seasonal conditions of the west coast which has subtropical north flowing ocean currents in the summer and in the winter the development of a south flowing wedge of tropical ocean water which extends from the north to about Cape Leeuwin. The distribution of marine coastal animals around Australia is determined by such combinations of basic oceanic water type, extent of terrestrial run off, sedimentation from the land and the nature of the land which is being eroded.

It is noteworthy that the combinations of environmental factors as indicated in Figure 2 fit remarkably well with the generally acceptable marine zoogeographic provinces of Australian coasts (Kott 1952, Bennett and Pope 1953, Endean 1957). Along the Pacific Queensland coast the effects of local climatic conditions have resulted in the recognition of two faunas—the coastal Banksian which is influenced by the terrestrial mud and the Solandrian which is offshore, clear of the mud, where the clear waters and coral reefs of the Great Barrier Reef provide the basic environment.

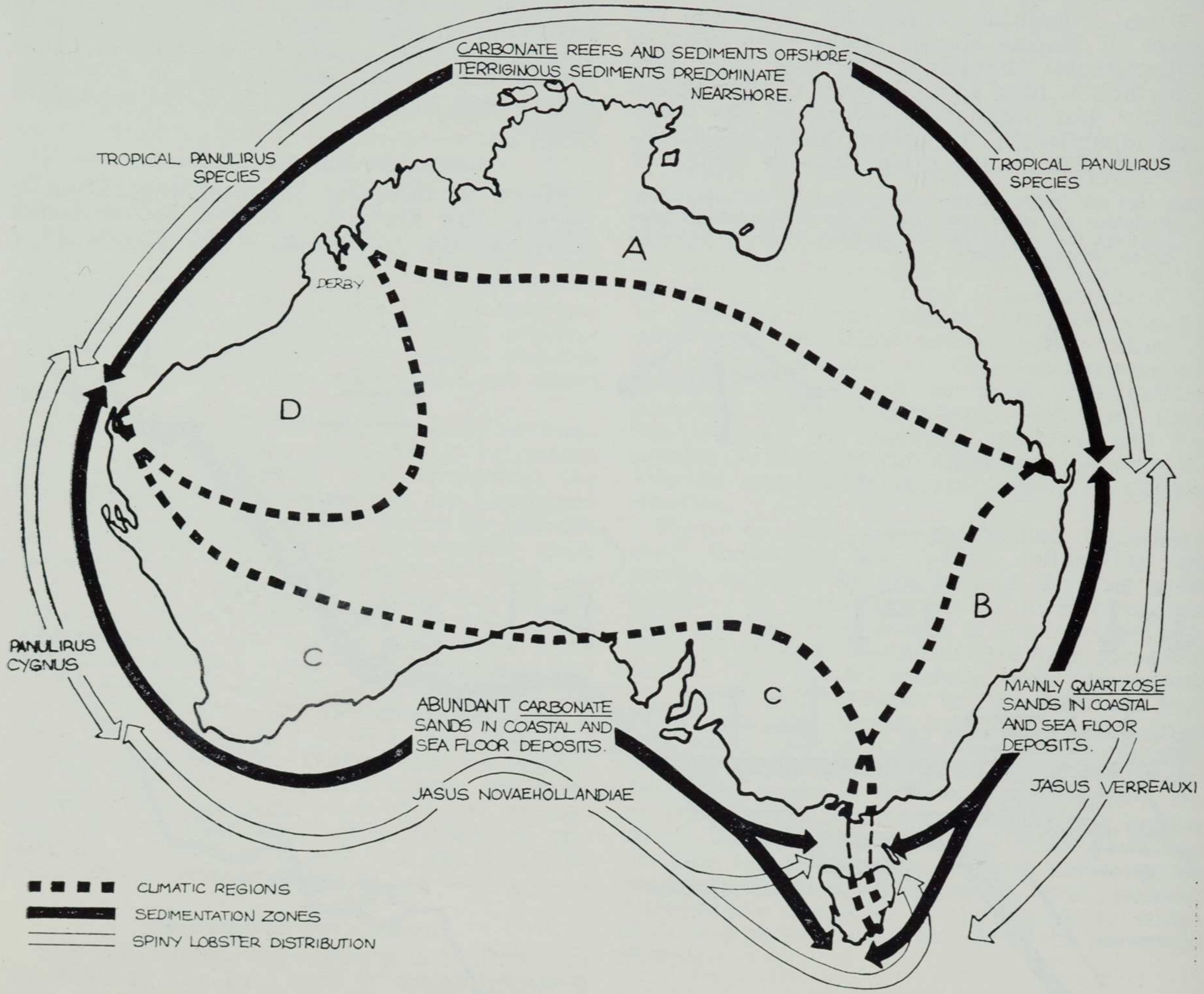

Figure 2.—Australian coastal climatic regions, coastal sedimentation zones and spiny lobster distribution. The types of sedimentation on the Australian continental shelf are taken from Brown (1968). The climatic regions were compiled from Thornthwaite (1931) (in Keast, 1959), Gentilli (1961) and Commonwealth Bureau of Census and Statistics (1966). The regional climatic classification is based on rainfall character which reflects the continental wind systems (Gentilli 1961 : 470)—A. Rainfall predominantly summer, reliable; B. Uniform rainfall throughout year, reliable; C. Rainfall predominantly winter, reliable; D. Rainfall during summer cyclones, winter dry, very unreliable. Note: Derby appears to be about the westward limit of *P. polyphagus*, one of the tropical *Panulirus* species.

Now let us look at the broad marine zoogeographic faunal zones described so well by Ekman, selecting again for our examples the spiny lobster. The zones for shallow water animals are the tropic, subtropic, temperate (all of which have spiny lobsters living in them) subpolar and polar. (Spiny lobsters also occur in subpolar regions but only as deep water species in depths down to 700 fathoms.)

The tropical northern Australian spiny lobsters are not endemic to Australia but form part of a vast fauna which is called the Indo-West Pacific fauna (Ekman, 1953). Many animals apparently have little difficulty in dispersing, either as adults or larvae, all along the extensive continental and island coasts of the Indian and western part of the Pacific Ocean. These tropical shallow water species are distinct from, but nevertheless quite similar to, the spiny lobster species in three equatorial faunas—the East Pacific, the West Atlantic and the East Atlantic (which extends to some degree into the Mediterranean).

The subtropic species of spiny lobster in Australia live along the west coast (*Panulirus cygnus*) and the lower east coast (*Jasus verreauxi*). *P. cygnus* is an Australian endemic and is closely related to other endemic subtropic Indo-West Pacific species in Japan (*P. japonicus*), Hawaii (*P. marginatus*), Easter Island (*P. pascuensis*) as well as the equatorial *P. longipes*. *J. verreauxi* occurs in the north island of New Zealand as well as the New South Wales coast and represents as a single species a distinct subgroup of *Jasus*.

On the south coast of Australia the fauna is mostly unique to Australia although very similar species occur on the other continents and islands at equivalent latitude in the southern hemisphere. The southern crayfish *Jasus novaehollandiae* is very closely related to the other *Jasus* species in New Zealand, Juan Fernandez, Tristan da Cunha, South African west coast, and St. Paul Islands. These species of *Jasus* form part of the circumpolar temperate marine fauna.

Although species of spiny lobster do not occur on the Subantarctic Islands to the south of Australia, clear faunal zones occur in these waters. On these Subantarctic Islands a circumpolar subpolar fauna is recognised and further south around Antartica there is a distinct polar fauna.

These latitudinal zones are determined by the physical characteristics of the water masses adjacent to those coastal regions, modified by any particular influences of the local land mass. One of the most obvious and most easily measured physical features of these water masses is the water temperature and the boundaries of these marine zones are usually defined by zoogeographers by water temperature values.

Vaughan's (1940) proposed marine zones were based on temperature and these zones certainly correlate with distribution of spiny lobster. But temperature as such does not serve to *separate* the 6 species of tropical spiny lobsters as temperature *appears to separate* the subtropic and temperate species.

Vaughan's zonation applied to the Australian and other regions mentioned above is as follows:

Polar	-1.9	to 5°C	Antarctic.
Subpolar	5	to 10°C	Subantarctic.
Temperate	10	to 25°C	South coast of Australia (1 sp. of spiny lobster).
Subtropic	15	to 30°C	West and lower east coast of Australia (1 sp. of spiny lobster in each area).
Tropic	25	to 31°C	North coast of Australia and Indo-West Pacific (6 spp. of spiny lobster).

So far we have been dealing only with the spiny lobsters in the shallow coastal waters, but they also show very clear evidence of vertical and latitudinal zonation as well (see George & Main 1967 Fig. 2). The vertical zonation broadly correlates with water temperature but once again we must note that temperature is a reflection of the total water mass the species lives in. For instance oxygen availability is probably far more important than actual temperature to marine animals whether in the deep sea or in the shallow waters. The sources of oxygen for the deep sea are in several specific surface regions of the oceans, i.e. north west Atlantic, Weddell Sea and other regions around Antarctica.

In those places, oxygen values are highest; the lower the value in the deep sea the "older" the water is thought to be. On this basis the "oldest" water is in the North Pacific, i.e. the oxygen has been used up by biological processes in its passage from the regions of the Anatractic to the North Pacific. Oxygen requirements for any one of the spiny lobster species is not known but whatever their requirements are, the evolutionary selection has been initiated by the very nature of the waters to which they are now adapted.

The next question is why are there so many *Panulirus* species in the shallow tropic regions compared with subtropic? This applies not only to the *Panulirus* group but as a general rule to all marine groups. Species diversity is a reflection of habitat diversity and the equatorial shallow water region certainly provides very many different sorts of habitats.

The following examples will adequately illustrate the wide range of habitats, determined for any region by the combination of the local oceanic water mass, the local climate and the local geography and geology. The region I have chosen is the Indo-West Pacific equatorial region.

1. Red Sea—barred deep basin with little water exchange with the Indian Ocean. Adjacent deserts and low river run off result in little sediment on coastal shelf and high evaporation. So waters are clear, warm and probably above normal salinity.
2. East Aden—open ocean with seasonal low water temperature because of upwelling. Waters clear in non-monsoon but very turbid in monsoon. Substrate fine sand of terrestrial origin. Normal salinity. Little coral growth.
3. Indian west coast—open Indian Ocean coast flooded in the northern part by the Indus River resulting in a trend from north to south from a muddy, seasonally flooded area to fairly clear, low run off area in the south.

4. Bay of Bengal—well established large rivers drain continuously from the Himalayas via the Ganges, the Irrawaddy and Brahmaputra Rivers. Salinity of the whole bay is very low (normal sea salinities are not met with until about south of approximately 10°N latitude). The huge volumes of sediment carried by the rivers make the bay more like a huge, deep silty estuary.

5. Arafura Sea, Gulf of Carpentaria and Timor Sea—these regions together form a semi-enclosed, shallow region, narrowly open to the east through Torres Strait and broadly open to the west. Moderate volumes of sediment and fresh water discharge result in a reasonably muddy marine environment, subject to regular flooding of the coastal rivers with some flow of oceanic water from the Pacific via Torres Strait.

6. Offshore islands—some terrestrial run off into the shallow waters and beyond the influence of the rivers, fringing coral or limestone reefs in crystal clear water. This is essentially the condition found along the Queensland north coast already mentioned, i.e. muddy coastal waters and clear coral waters offshore.

These examples illustrate the contrasts in habitat provided in this equatorial region of fairly uniform water temperature. But we see that in spite of these fairly uniform water temperatures different yet reliable habitats are present. An assessment of the degree of reliability of a habitat is paramount in the full understanding of past evolutionary events in the "life" of a species.

Now where do the tropical species of *Panulirus* fit into these habitats? In the Red Sea *P. penicillatus* predominates in those clear waters. In East Aden one species, *P. homarus,* dominates in the cooler, slightly turbid waters. In the very muddy coastal waters off Karachi, *P. polyphagus* is the most common species and as one proceeds south along the west coast of India other species dominate. The order of relative abundance proceeding south is *P. polyphagus, P. ornatus, P. homarus, P. versicolor, P. longipes* and *P. penicillatus.* The very low salinity waters of the Bay of Bengal have few records of crayfish at all; the only records of note are from the Andaman and Nicobar Islands which are well offshore. In the Arafura Sea, Gulf of Carpentaria and Timor Sea to the north of Australia there are probably many more prawns than spiny lobster but one species, *P. polyphagus,* appears to be the most common spiny lobster. It has been trawled in low numbers in Joseph Bonaparte Gulf. Records of other species of spiny lobster in Western Australian northern waters follow the habitat trend in turbidity illustrated on the west coast of India. These results have been published recently (George 1968). In the offshore islands of the Pacific, *P. penicillatus* and *P. longipes* are the main species in the clear waters with some occurrences of *P. ornatus* or *P. versicolor* if enough of the right kinds of sediment is available.

Evolution of Palinuridae

For many of the extant palinurids, environmental changes have resulted in little radiation even though they are relatively old groups. George and Main (1967: 813) suggest that for these deeper water primitive groups "the geological and oceanic barriers which divided the once continuous equatorial seas of the world (including the Tethys Sea) into the present day faunal regions fragmented the early stocks, and that the subsequent morphological changes in these groups were very slow". For the deep water genus, *Puerulus,* for example, living in the isolated deep water basins, each of which probably has a peculiar environmental character, one can imagine the difficulty of altering the oxygen content or the temperature or the salinity or the substrate without a major upheaval of the ocean's circulation patterns.

We can more easily imagine changes which would influence the evolution of a more recent (but not the most recent) group like *Jasus.* This genus is at least as old as the lower Miocene (Glaessner 1960) and the evolution of this circumpolar group of species is best explained by shifts of the southern circumpolar temperate belt into higher latitudes. Such a shift would alter the geographical position (but not necessarily the physical characteristics) of the marine temperate zone as recognised today. Six species live in this zone; on the south coast of Australia *(J. novaehollandiae),* New Zealand *(J. edwardsi),* Juan Fernandez *(J. frontalis),* Tristan da Cunha *(J. tristani),* south west coast of Africa *(J. lalandii)* and St. Paul's Island *(J. paulensis).* A very distinct species, outside this group of species, lives on the New South Wales coast and in the north of the North Island, New Zealand—*J. verreauxi.*

There is good evidence of much warmer conditions prevailing in the past. Cowen summarises (p. 182) the earth "has been relatively warm and moist throughout much of geological time. For 90 per cent of the past half billion years . . . . . its average surface temperature has been 72° Fahrenheit in contrast to the present average temperature of 58°. Tropical and subtropical climates prevailed to high northern and southern latitudes".

How might the present species of *Jasus* have originated? In warmer times the parent species of the *Jasus* group would have been much further south, occupying a circumpolar distribution in the present geographic position of the Subantarctic Zone. The present Subantarctic Zone lies between about 45-55° S. latitude and a fairly uniform marine fauna is recognised on the coasts of these islands and continents. Powell (1965 p. 352) for instance describes three major marine provinces for molluscs within the Subantarctic.

The Magellan: Patagonia west coast to Chiloe I., east coast to C. Blanco and the east Patagonian Continental Shelf including Falkland Islands and Burdwood Bank.

The Kerguelenian: Kerguelen, Crozet, Marion, Prince Edward and Macquarie Islands.

The Antipodean: Auckland, Campbell, Antipodes and Bounty Islands.

This would have been the approximate geographical distribution of the parent *Jasus* species and the water would have been temperate in character rather than subpolar. The West Wind Drift was probably still present but perhaps weaker than present and in those latitudes it would be a suitable transport mechanism for the pelagic larvae especially if they clung to flotsam. Large seaweed rafts float eastward under the influence of the West Wind Drift and are characteristic of these latitudes today.

With a general cooling, i.e. a shift to lower latitudes of waters with today's temperate environment, geographic isolation of the parent *Jasus* stock would be likely on the coasts of the southern continents and on mid latitude island groups. Natural selection would operate against very long larval life under these conditions and a shortening of the larval life would become an advantage. The possible pathways which lead to these isolations would be influenced by the direction and strength of the currents, the availability of relatively shallow water and the length of larval life. Isolation is envisaged as follows:

(a) the *frontalis* population moving northward up the west South American coast, responding to the present northward sweep of the West Wind Drift up the South American coast and responding to the selection pressures of the "marine climate" of the St. Ambrosius-Juan Fernandez region

(b) the *lalandii* population moving north and east via the Mid Atlantic and Walvis Ridges to the west coast of South Africa, responding to the northward sweep of the West Wind Drift up the South African coast. It is now responding to the regular marine environment produced by the Benguela Current.

(c) the *tristani* and *paulensis* populations moving to the north via the Mid Atlantic, the Atlantic-Indian and the Mid Indian Ridges under the influence of northerly offshoots of the West Wind Drift.

(d) from the Macquarie Antipodean region, the *novaehollandiae* population migrating to the south coast of Australia via the South Tasmanian Ridge and the *edwardsi* population taking up their present position on the main islands of New Zealand and Chatham I. by way of the Campbell Plateau. The major selective factors which maintain isolation of these two species today are the distinctive bottom substrates and patterns of water circulation around southern Australian and New Zealand coasts.

The other species of *Jasus (J. verreauxi)* which today lives in subtropic temperatures probably always occupied a geographic position in waters to the north of the *J. lalandii* group just discussed. Indeed a lower Miocene fossil remarkably close to *J. verreauxi, (J. flemingi)*, has been recorded from Nelson in New Zealand, a locality much further south than the present day distribution of *J. verreauxi* (Kensler 1968). Perhaps at that time the *J. verreauxi* parent species occupied the present geographic range of *J. edwardsi* when the *J. edwardsi* parent species was further south on the New Zealand subantarctic islands.

In the equatorial warm waters, one genus *Panulirus* is dominant and radiation has been the most rapid and the most recent of all palinurids (George and Main 1967). These workers have pointed out that in the Cretaceous and early Tertiary similar radiations of spiny lobsters occurred as evidenced by the abundant shallow water fossils of *Linuparus* for example. The simplest explanation for the rapid evolution of species in these tropical regions is to have development of "new" habitats. Geographic areas in the tropics are the most likely to have changing habitats with slight changes in climatic conditions and with these changes "new" habitats can form. We have seen how some of these geographic regions—Red Sea, East Aden, Indian west coast, Bay of Bengal, and Arafura Sea-Gulf of Carpentaria-Timor Sea region have their characteristic habitats maintained under the present climatic conditions. And we have also seen how the separate species of *Panulirus* in the Indian and West Pacific Oceans preferentially occupy these habitats. It is suggested here that those habitats are of relatively recent origin (perhaps with the warming of the waters after the Pliocene) and that the fluctuations of climate and ocean currents during the Pleistocene have resulted in contractions and expansions of species range and isolations and reconnections across ocean "barriers" and terrestrial isthmuses.

If the present day region of most suitable habitat for a species was in fact its geographic origin, I venture the following suggestions for the tropical *Panulirus* species of the Indo-West Pacific. *P. penicillatus* was originally isolated in the Red Sea and that natural selection operated in favour of individuals best adapted to clear water unaffected by organic or terrestrial sediments. *P. homarus* arose off the west coast of the Arabian Sea in response to the proximity of the oceanic, cooler waters caused by coastal upwelling and the nature of the terrestrial sediments. *P. ornatus* may have evolved along the East African coast in response to the conditions determined by the particular nature of the organic sedimentation there. *P. polyphagus* with its affinity for river mud could have initially separated in response to the Indus system which is reasonably reliable in character since it originates in the Himalayas. *P. versicolor* could have originated in a warm water area adjacent to live coral areas but not necessarily in the live coral itself. These conditions prevail on the north coast of Western Australia between Roebourne and Broome where sediments from the Great Sandy Desert blow into coastal waters and where tidal movements stir up these sediments (see George 1968).

If these origins are correct then distributions of species to regions outside these main centres occur where similar environmental conditions exist. When a period of climatic change stresses the species, the species range would be expected to contract towards the most ideal (and presumably the original) geographic region. Periods of expansion would also be expected if suitable habitats are provided in additional areas. But a change in one set of climatic conditions may result in expansion of one species but adversely affect other species which would contract their range. Increased rainfall and sediment discharge would expand the range of *P. polyphagus* near the rivers but would cause *P. penicillatus* (Red Sea) to contract its range since the waters would contain more terrestrial sediment.

Conclusion

The state of knowledge about the distribution, taxonomy, ecology and phylogenetic interpretation of marine animal groups is not as complete as for the terrestrial groups. Nevertheless, the same principles of isolation and subsequent speciation must apply and by using marine spiny lobsters as an example I have attempted to suggest how these principles may account for the present distribution of a particular marine group of animals. The effect of environmental change is one of the most important concepts in any explanation of the distribution of both marine and terrestrial animals in space and in time since the total environment (the climate) constantly selects for animals best suited to meet that set of environmental parameters. Changes in climate patterns directly and immediately alter the value of previous selective advantages.

I would like to summarise the opinions I have presented in this paper as follows:

1. A marine climate exists under the sea and this operates in the same manner in the distribution of marine animals as the terrestrial climate operates on terrestrial animals.
2. For the coastal species of spiny lobsters, their marine climate is determined by such factors as coastal morphology, terrestrial rainfall, submarine geology and adjacent terrestrial geology, adjacent circulation of ocean water masses.
3. Combinations of these factors provide numerous distinct spiny lobster habitats, isolated from one another by the regional peculiarities.
4. The coastal habitats in the tropics are much more easily changed by climatic events than coastal habitats in higher latitudes or deep water habitats.
5. In the shallows of the tropic region, speciation is more rapid than in other regions and in this sense is an "origin for species" but not a centre from which these species are despatched to other regions with different environments.
6. Evolutionists must assess the biological attributes which natural events have selected in the past evolution of the species examined so that the most likely means of isolation for their studied species can be proposed.
7. *Jasus* species probably became geographically separated on the coasts of the southern continents and islands after the stock (as one circumpolar species in the present Subantarctic region) moved north to the lower latitudes with a climate cooling.

Acknowledgements

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